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STUDIES ON THE GEOTROPISM OF THE MARINE SNAIL, *LITTORINA LITTOREA*.¹

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I. INTRODUCTION.

In 1888, Loeb pointed out that "Die Schwerkraft der Erde, wenn sie senkrecht gegen die ventrale Seite der Schabe gerichtet ist, wirkt als Reiz, der dieselbe zu Bewegungen veranlasst" (8, p. 9). Since then, with modifications of his method, Davenport and Perkins (2) and Frandsen (3) have investigated the same problem on a slug, *Limax maximus*. The former drew the conclusions that, "the precision of orientation of the slug varies directly with the active component of gravity" (2, p. 105) and that "this tendency (to go either up or down) must be ascribed to some internal condition of the individuals, for it varies in different individuals and in the same individuals at different times" (2, p. 110). The latter reached rather different conclusions, thus: "The different geotactic response, on a glass plate, of different individuals is due mainly to two factors: (a) The quantity and quality of the slime secreted, which is a very important factor; (b) the relative proportions of the length of the

¹ From the Marine Biological Laboratory, Woods Hole, Mass., and the Physiological Laboratory, University of Minnesota, Minneapolis, Minn.

anterior and posterior regions of the animal's body. All the conditions being the same, it is this factor which 'determines whether the head end will be directed up or down'" (3, p. 205).

The reactions of the marine forms of *Littorina littorea*, *L. rudis*, etc., to light and other influences have been studied by Mitsu-kuri (12), Bohn (1), Haseman (4), and Morse (14). Unfortunately, however, none of them has taken into consideration the response of the animals to gravity, although the effect of gravity upon *Littorina* and upon gastropods in general is remarkable and easily observed at the seashore.

Following the example of Frandsen and of Davenport and Perkins, an attempt was made by the writer with *Littorina littorea* to determine: (1) "What relation exists between a variation in the pressure of gravity and the precision of orientation?" and (2) What "determines whether the head end will be directed up or down?"

The experimental work was done in the physiological department of the Marine Biological Laboratory at Woods Hole, Mass., during the summers of 1912 and 1913. The results obtained in 1912 used in this paper are indicated by the date, "1912." The others were all secured in 1913.

II. MATERIAL AND METHODS.

1. *Material*.—The animal used in all the experiments was a marine snail, *Littorina littorea*, which is numerous about Woods Hole. The snails were collected by the writer in the morning or afternoon, just before a new series of experiments was carried on, and were kept in a large glass dish in running sea-water during experiments. The size of the animal used was about 1.5 x 1.1 cm.¹ It was found that this was the more convenient size for experimental purposes, because the bigger, *i. e.*, older, ones retreated into and remained for a long time in their shells when handled. The younger animals are more active and quicker to respond to stimuli.

The same individuals could not be used throughout any series of experiments; since their movements became abnormal, due

¹ The laboratory collector, Mr. Gray, told me that the snails which I used were about one year old.

possibly to fatigue. The same individuals could be used only for four or five trials. Ten individuals, sometimes 11 or 12 (with anticipation of falls), were used for each trial of a series of experiments. As will be seen in the tables, however, very often less than 10 individuals were left on the support for observation, the rest having fallen down.

2. *Methods*.—Loeb's method (8) modified by Davenport and Perkins (2) and by Frandsen (3), of the different angles of inclination of a support, on which the animals are to be placed, was adopted with variations. The support was a plain glass plate about 22 x 19 cm., marked off on one side into squares of one sq. cm. each, whereby it could be readily determined how far the animals moved from their original places.

The support, or plate, was placed in an apparatus by which it could be held at any ten-degree angle between the horizontal and vertical (see Fig. 1).

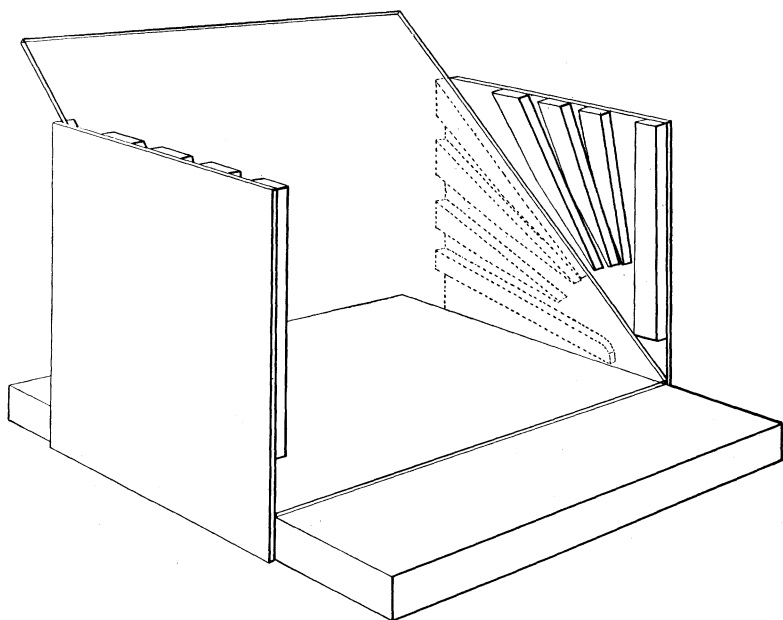


FIG. 1. G. P. = a plain glass plate. The rest of the apparatus is all wood.

The animals were placed on the unlined side of the plate, moistened and held upside down at an inclination, say 10° to

the horizontal, so that their heads were all directed upward. Meanwhile sea-water was poured, two or three times, over the animals and the plate surface to prevent their moving before the commencement of the experiment, and at the same time to get them to stick tightly to the surface. When the desired number of individuals had been so placed, the support was reversed, and placed at the desired angle in the holding apparatus, so that their heads were, now, directed downward. The animals being negative to gravity, this procedure was necessary in order to determine their movements of orientation in a desired time.

Experiments were conducted either in sea-water in a glass aquarium, or in air. To exclude the effect of light in either case, a square box painted black inside was employed to cover the whole arrangement described above.

After the desired time for a particular experiment, the cover-box was removed. Then the movements which the animals had made were recorded (with detailed notes) as nearly as possible as follows: A movement of 180° from the original was designated as "oriented"; 90° as "horizontal"; and 0° as "original." If an animal was observed to have crawled downward from the original place, it was recorded as positive to gravity. It was noticed that some individuals did not crawl downward quite vertically, but no discrimination as to these is made in the tables. Quite a few individuals, that crawled horizontally, are also arbitrarily classified under "horizontal," although such movements are believed by the writer to have no great significance.

A question might be raised about middle spaces between 180° and 90° , and also between 0° and 90° . Such positions were seldom observed; but if any were observed, they were recorded as "oriented" at a position between 90° and 180° ; as "horizontal" between 90° and 45° ; and as "original" between 45° and 0° . Moreover, since quite a number of individuals would possibly have become oriented if they had been given longer than one minute, it might have been better to describe them as "orienting" rather than "horizontal." The animals whose position was specified as "original" should not be interpreted as indifferent to gravity. They simply failed to respond to it during the time

when they were under experimentation. The time factor was important. This will be confirmed by the following preliminary experiment *A*. But for the more detailed study, the shortest possible time was adopted, to avoid fatiguing the animals.

In all the following tables, the signs indicate positive either to gravity or light by + and negative by -.

III. EXPERIMENTS.

1. *Preliminary Experiments with Gravity and Light.*

Preliminary Experiment A.—A tall beaker full of sea-water was placed upside down in a large dish filled with sea-water. Special care was taken to exclude air bubbles from the beaker. It was then supported on two pieces of glass-tubing about 4 mm. in diameter in the dish in order to let the sea-water within communicate freely with the outside at the bottom. By means of glass-tubing, sea-water was run into the dish so as to have fresh sea-water always at the bottom, but so as not to let any air bubbles into the beaker. Thirty selected snails were placed under the beaker, and between the two pieces of the glass-tubing, which was not high enough to permit the snails within to crawl out from under the beaker. The whole arrangement was then covered with the box already described, to exclude light.

About ten minutes later it was found that all the snails had crawled up the vertical (inside) wall of the beaker and gathered at or near its top. The sea-water would be expected to be fresher and better supplied with oxygen at the bottom than at the top. The snails, however, crawled upward just the same. This was repeated several times, but there was no exception to this rule.

Such results indicate that the upward movements of the snails are not caused by the lack of oxygen but by gravity. This is also fully supported by the fact that the snails crawl upward on moist rocks, or on a moist glass plate, in air where the amount of oxygen does not vary.

Moreover, in leaving the horizontal bottom of the dish to take positions on the vertical wall of the beaker, the snails must have oriented themselves against the pull of gravity. This orientation of the snails cannot be explained by the mechanical theory of geotropism. It is an active process, one of true response to

stimulation. Loeb's conclusion which was already referred to, is thus confirmed.

Preliminary Experiment B.—According to Bohn and Mitsukuri, *Littorina littorea* is negatively heliotropic. To test their results, a simple method of "righting" experiments was adopted as follows:

Ten selected individuals were placed dorsal side down on each of two glass plates. The one was covered with the box, and at the same time, the other was exposed to diffused daylight, both for five minutes. The two lots were alternately covered and exposed to daylight, after the animals had been refreshed in sea-water and again turned "on their backs." The results given in Table I. show that light considerably affects the "righting" response of the animals.

TABLE I.

THE "RIGHTING" OF SNAILS ON A HORIZONTAL GLASS PLATE IN DARKNESS AND DAYLIGHT FOR FIVE MINUTES (1912).

No. of Trials.	No. of Animals.	Darkness.		No. of Animals.	Daylight.	
		Righted.	Not Righted.		Righted.	Not Righted.
I	10	4	6	10	3	7
I	10	8	2	10	2	8
I	10	6	4	10	3	7
I	10	5	5	10	2	8
I	10	6	4	10	3	7
I	10	6	4	10	2	8
I	10	4	6	10	4	6
I	10	4	6	10	2	8
I	10	5	5	10	3	7
I	10	4	6	10	2	8
Total. . 10	100	52 or 52%	48 or 48%	100	26 or 26%	74 or 74%

In explanation of this "righting" reaction of the snails, it may not be out of place to refer to Loeb's analysis in the starfish. According to him, the "righting" of the starfish is a stereotropic phenomenon, but not geotropic (10, pp. 64-65). Recently Moore confirms this conclusion through experiments (13, p. 237), while Jennings seems to have been misled in this respect (5, pp. 120-148). The "righting" of the snails may also be a stereotropic phenomenon, though it makes no difference for the present purpose. In fact, however, as will be seen later, contact stimuli interfere with the snails' reaction to gravity. The main point in

regard to Preliminary Experiment *B* is that light is a factor in the behavior of these animals.

Preliminary Experiment C.—According to the “mechanical theory” of geotropism, an animal becomes oriented head up because of its heavier posterior region, or it orients itself with its head down, because of its heavier anterior region or head. An experiment was, therefore, made to determine which region of the snails, the anterior or the posterior, was heavier. This was simple. When an individual was placed on a glass plate in seawater with its dorsal side down, it came out of the shell, and made an “effort” to “right.” It was then carefully dropped and watched as it sank, before it retreated into the shell. Every one of them sank with its anterior region up, as expected. The was done also with those individuals which were positive to gravity at a certain angle of inclination. There was, however, no exception.

With the same point in mind, empty shells were tested. One of them was fixed by its ventral side on a small square cover glass, with as little glue as possible. At the three corners of the cover glass, fine threads were fastened. The center of gravity was found by suspension to be located somewhere in the posterior region. This was done with a number of shells and the same results were obtained in every case. These results, therefore, agree with the other observations, indicating that the posterior region of the snails is heavier than the anterior region.

From the above results, the writer is justified in concluding that the center of gravity of the snails is located in the posterior region; and a possible inference from this conclusion is that the posterior region of the snails has a greater specific gravity than the anterior region. This fact and inference may have a bearing in deciding whether the orientation of the animals against gravity is due to purely physical or mechanical pull. This question will be considered throughout all the following experiments.

2. *Experiments to Show the Relation between the Pressure of Gravity and the Precision of Orientation.*

Experiment A.—Davenport and Perkins asked and answered by experiment: “What relation exists between a variation in the

pressure of gravity and the precision of orientation of the slug?" (2, p. 100). An attempt was made by the writer to determine experimentally the same question for *Littorina littorea*. The experiments were conducted in sea-water. Light was excluded by means of the cover-box. The results given in Table II. show that the higher the angle the larger is the number showing *negative* geotropism, and the lower the angle the larger the number of (so-called) *positively* geotropic animals.

TABLE II.

GEOTROPISM OF SNAILS AT THE DIFFERENT ANGLES OF INCLINATION OF A GLASS PLATE IN SEA-WATER IN TOTAL DARKNESS.

At beginning of experiments each head pointing downward. Table shows results after one minute.

Temp. of Sea-water.	Angles.	No. of Trials.	No. of Animals.	- Geotropism.				+ Geotropism.		Did Not Move.	
				Oriented.		Horizontal.		Crawled Downward.			
				No.	%.	No.	%.	No.	%.	No.	%.
18½°-21° C.	90°	35	300	300	100	0	0	0	0	0	0
18½°-18½° C.	78½°	22	200	200	100	0	0	0	0	0	0
18½° C.	67½°	22	200	190	95	3	1.5	5	2.5	2	1
19°-19½° C.	56½°	23	200	180	90	9	5.5	7	3.5	4	2
19½°-19½° C.	45°	25	200	163	81.5	13	6.5	12	6	12	6
19½°-20° C.	33½°	32	200	152	76	15	7.5	16	8	17	8.5
19½°-20° C.	22½°	33	200	130	65	22	11	23	11.5	25	12.5
20°-20½° C.	11½°	23	200	110	55	26	13	34	17	30	15
Total.....		215	1,700	1,513 or 89%				97 or 5.7%		90 or 5.2%	

As already pointed out, however, it is misleading to consider that the negative geotropism of the snails reaches zero on the horizontal surface of the earth. The force of gravity stimulates the snails, when it happens to pull along the line of the dorso-ventral axis of the animals, that is, on the horizontal surface, as the preliminary experiment *A* has shown. But the larger the angle the shorter the time required for orientation. This is shown in the "horizontal" column, when the number of the animals, most of which were "orienting" at the end of one minute, decreases as the angle of inclination to the vertical increases.

Experiment B.—It has been supposed that hydrostatic pressure affects the reaction of an animal to gravity. To decide this question, a series of experiments was made in air. Light was

excluded as usual. The results given in Table III. show an interesting difference compared with those of Table II., which must not be overlooked. The number in the negative geotropism column in Table III. is always higher than the corresponding one in Table II., and that in the positive column in the former is always lower than that in the latter. A possible explanation of these differences is found in the buoyancy effect of the water, which decreases the weight of the animals. In consequence, the pull of gravity is more effective on the animals in air. It would seem therefore that the pull of gravity on the animal as a whole must be one factor in its orientation.

TABLE III.

GEOTROPISM OF SNAILS AT THE DIFFERENT ANGLES OF INCLINATION OF A GLASS PLATE IN AIR IN TOTAL DARKNESS.

At beginning of experiments each head pointing downward. Table shows results after one minute.

Temp. of Room.	Angles.	No. of Trials.	No. of Animals.	— Geotropism.				+ Geotrop.		Original.	
				Oriented.		Horizontal.		Crawled Downward.		Did Not Move.	
				No.	%	No.	%	No.	%	No.	%
21 $\frac{3}{4}$ °–22 $\frac{1}{2}$ ° C.	90°	20	100	100	100	0	0	0	0	0	0
25° C.	78 $\frac{3}{4}$ °	14	100	100	100	0	0	0	0	0	0
22 $\frac{1}{2}$ °–23° C.	67 $\frac{1}{2}$ °	15	100	100	100	0	0	0	0	0	0
23° C.	56 $\frac{1}{2}$ °	13	100	92	92	2	2	2	2	4	4
23 $\frac{1}{2}$ ° C.	45°	13	100	86	86	6	6	6	6	2	2
21 $\frac{1}{2}$ ° C.	33 $\frac{3}{4}$ °	17	100	80	80	8	8	9	9	3	3
22 $\frac{3}{4}$ °–23° C.	22 $\frac{1}{2}$ °	13	100	67	67	13	13	18	18	2	2
22° C.	11 $\frac{1}{4}$ °	14	100	60	60	13	13	27	27	0	0
Total.		119	800	727 or 90.8%				62 or 7.7%		11 or 1.3%	

The above fact reminds the writer of the “mechanical theory” (6, pp. 2–13) and, also, the “resistance or weight theory” (6, pp. 14–20) of geotropism in *Paramecium*. If the greater weight of snails in air causes the quicker orientation of the animals, and also if the posterior region of the animals is heavier than the anterior region (as has been proven to be the case), the theories above mentioned are favored to some extent. Nevertheless, no mechanical theory can satisfactorily explain why “positive geotropism” increases with decrease in the angle of inclination. This, if a real gravity response, must be explained on the basis of physiological conditions, as Loeb pointed out many years ago.

The question, however, arises: Is there any maximum or minimum of resistance or weight which makes the snails crawl either up or down? This question will be answered later.

Although differences exist between Tables II. and III., the results in the latter table in general show a fair uniformity with Table II. The hydrostatic pressure,¹ therefore, seems seldom, if ever, to affect the negative reaction of the animals to gravity. These two tables also show a fair agreement with the results obtained by Loeb (8, pp. 6-8), Davenport and Perkins (2, pp. 100-105), and Frandsen (3, p. 198), that is, a steady increase in negative geotropism with increase in the angle of inclination. Davenport and Perkins's view in this respect is fully confirmed (2, p. 105).

3. *What Determines Whether the Head End Will be Directed Up or Down?*

Experiment A.—Instead of the plain glass plate used for experiments hitherto, a ground-glass plate was employed for the following experiments, for two reasons: (1) Since the animals live along a rocky seashore, the plain glass plate may not be a proper support for them; and (2) the animals being positively stereotropic, it was thought well to test the effect of contact stimuli upon their geotropism. Light was excluded in these experiments as usual. In the results given in Table IV. it is interesting to note, as expected, a decided decrease in the number of negatively geotropic and an increase of "positively geotropic" individuals with decrease in the angle of inclination. Moreover, below the 45°, no individuals were in their original position.

The animals can stick better to the ground plate than they do to the plain glass. In consequence, they can resist the pull of gravity better on the former than they do on the latter. If so,

¹ On preparing Mr. Kanda's Ms. for publication it strikes me that the chief difference between the experiments shown in Tables II. and III. lies in the buoyancy rather than the pressure factor. Remembering that the air pressure must be added to that due to any depth of water, the difference in pressure in Table II. as contrasted with III. is almost negligible. But the weight of the animal in water is much less than in air. The slight difference between Tables II. and III. is to me strong evidence against the buoyancy theory as playing any large part. Mr. Kanda is in Japan and I cannot call his attention to these points, so I venture to add this footnote.
—E. P. LYON.

this serves to indicate that resistance plays a part, particularly in negative geotropism. The resistance theory, however, does not explain why the animals leave the horizontal surface on which they are placed and crawl upward on the vertical wall of a beaker (see preliminary experiment). This fact is unexplained by any mechanical or resistance theory.

TABLE IV.

GEOTROPISM OF SNAILS AT THE DIFFERENT ANGLES OF INCLINATION OF A GROUND-GLASS PLATE IN AIR IN TOTAL DARKNESS.

At beginning of experiments each head pointing downward. Table shows results after one minute.

Temp. of Room.	Angles.	No. of Trials.	No. of Animals.	- Geotropism.				+ Geotropism.		Original.	
				Oriented.		Horizontal.		Crawled Downward.		Did Not Move.	
				No.	%.	No.	%.	No.	%.	No.	%.
22½°-22¾° C.	90°	14	100	100	100	0	0	0	0	0	0
22° -22½° C.	78¾°	16	100	96	96	0	0	2	2	2	2
22¾°-23° C.	67½°	13	100	82	82	6	6	10	10	2	2
23° -23½° C.	56¼°	13	100	71	71	10	10	16	16	3	3
27° C.	45°	12	100	63	63	12	12	25	25	0	0
25¼° C.	33¾°	11	100	53	53	13	13	34	34	0	0
24¾°-25½° C.	22½°	10	100	39	39	20	20	41	41	0	0
24¾°-25¾° C.	11¼°	10	100	23	23	22	22	55	55	0	0
Total.....		99	800	610 or 76.2%				183 or 22.8%		7 or .8%	

Experiment B.—A few experiments were made to determine the effect of a dry surface at the angle of 90°. The animals experimented on were carefully dried on filter paper. They were placed on a dry smooth glass plate with their heads directed *upward*. Light was excluded and the animals examined after two minutes. The movements of the animals on the plate were readily seen by the tracks of the mucus secreted by them.

Of 60 animals used 31 dropped off, 6 or 15 per cent. of the remainder oriented and crawled down, 31 or 79 per cent. crawled upward and one crawled horizontally. The striking fact is the number of individuals that oriented *positively* and crawled down. This evidence goes to show that the animals tend to become positive on a dry surface, which would evidently serve as a protective reaction when they are left on rocks by a retreating tide.

The movements of the animals on the dry plate were regular

in some cases and irregular in others. The figures given are, therefore, somewhat arbitrary. To avoid this inaccuracy, a few typical examples of movement are shown in figures as follows:

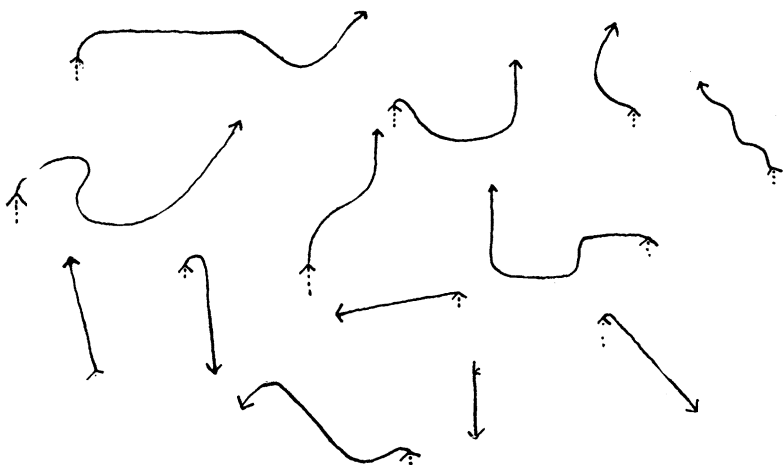


FIG. 2.

The arrows in the figure indicate the movements during the experiment, and the dots the movements of the animals after being placed on the plate but before the commencement of the experiment, *i. e.*, before the plate was covered by the dark box.

One thing is clear. Some of the animals on the dry glass plate and also those placed on a dry wooden plate, in an experiment the results of which will be seen shortly after this, oriented themselves and crawled downward, in spite of the mechanical difficulties due to their shells.

Experiment C.—In the next series, a dry wooden plate was used instead of the dry glass plate, in the same manner as in the above experiment. Of 60 animals used 24 dropped off, 19 or 52 per cent. of the remainder oriented and crawled downward, 6 or 16 per cent. crawled up and 4 crawled horizontally. Positive instead of negative geotropism was dominant, even though the experiments were conducted at the angle of 90° .

Experiment D.—The following series was of the same nature, except that the animals were placed with their heads down, and the time of experimentation was limited to one minute. Of 60 individuals used 33 dropped, 21 or 77 per cent. of those remaining

on the plate crawled downward; only 2 oriented negatively and these did not crawl upward; 4 failed to move. As the animals were not compelled to orient themselves in order to move down, the highest percentage of positive geotropism (21 individuals out of 27 or 77 per cent.) was obtained in this case.

That the character of the surface played a part is evident. But some explanation is necessary. When the cover-box was removed, nine individuals which had crawled down as shown by the mucus were found with the head end of their shells directed vertically, or with slight inclination to the vertical, *i. e.*, their shells mechanically "oriented" *upward* by the "greater pull of gravity" on the "heavier posterior region." Those individuals probably could not resist the pull of gravity and keep their shells from falling by their weight, while others could. Four individuals crawled downward not quite vertically (on a diagonal line between vertical and horizontal). It may be possible to explain this as a movement which was resultant of the pull of gravity on their shells and on themselves,—the resultant of a passive tendency to orientation and an internal response to gravitation.

From the above observations, one may explain the habitat of the snails, "which usually live on rocky surfaces which lie between the high-tide mark and one foot below the low-tide mark." The limitation of upward movement is due chiefly to the exhaustion of moisture carried by their "foot" from the sea. They seldom, if ever, crawl on dry rocks much higher than high-tide mark, though they do crawl on rocks clear out of sea-water. They seem to stop crawling when the moisture, which they carry with themselves, is exhausted. This agrees with Mitsukuri's and Haseman's observations.

It is not thinkable that either the dry glass plate, or the dry wooden plate makes it easier for the snails to become oriented and to crawl downward, than the ground-glass plate did. Nevertheless on the former surfaces many animals oriented themselves and crawled downward against the resistance of the heavier weight of their posterior region. If this is true, then the upward and downward movements of the snails can not be explained either by the resistance factor or the weight factor or by the both.

One thing is, of course, possible, that "the quantity and quality

of the slime secreted" makes it easier for the animals to crawl downward or upward, as Frandsen thinks in the case of slugs (3, p. 205). The question, however, arises: Why, then, did not the snails crawl upward instead of downward on the the dry glass and wooden plates?

In this respect, Parker and Parshley offer a suggestive explanation in the case of earthworms: "In the earthworm, the response to dryness . . . is apparently the selective extraction of water from the peripheral protoplasm of the worm, a process which is favored by capillarity of dry surfaces over which the worm begins to creep and is probably dependent chiefly upon evaporation from the surface of the worm itself. Under such circumstances, the materials in the peripheral protoplasm of the prostomium must become concentrated and probably initiates stimulation by undergoing some such change as partial coagulation" (15, p. 363).

If so, the explanation must be looked for in physiological conditions, that is, internal, rather than external mechanical factors. As Parker and Parshley explain, the dryness of the surface may cause the partial coagulation of the materials in the peripheral protoplasm of the "foot" as well as of the anterior geo-sensitive region of the snails, which may also result in surface-tension changes and contraction of "muscle elements," and cause the motion of displacement or coalescence of the fluid materials in the protoplasm of the muscle-fibers and internal cells (as Lillie thinks; 7, pp. 252-255), which possess different specific gravities. Under such circumstances, we may assume a disturbance in the peripheral as well as internal cells, especially perhaps in the cells of the geo-sensitive region or the geotropic organs, statocysts, which disturbance may be assumed to stimulate and cause the response of the animals. Whether the animal will go up or down will depend on the other stimuli besides gravity, such as character of surface and degree of dryness which accompany the stimulation of gravity itself. This view quite agrees with Loeb's (9) and Lyon's (11 or 6, pp. 20-21).

4. *The Effects of Light and Surface-film of Sea-water.*

Experiment A.—Experiments were conducted in the aquarium already described, which was closely surrounded by a four-fold black cloth, all over the sides and bottom. The snails were placed on the glass plate about 2.5 cm. below the surface film of sea-water. Part of the glass plate extended above the surface. By this arrangement, it was possible at the same time to test Haseman's conclusion that the upward and downward movements of the animals "are not due directly to either geotropism or phototaxis, but to the action of the film of water" (4, p. 113). The results are given in Table V.

TABLE V.

GEOTROPISM OF SNAILS IN AND OUT OF SEA-WATER IN DIFFUSE DAYLIGHT AT DIFFERENT ANGLES OF INCLINATION OF A GLASS PLATE.

At beginning of experiments each head placed pointing *downward*. Table shows results after one minute.

Temp. of Sea-water.	Angles.	No. of Trials.	No. of Animals.	— Geotropism and + Heliotropism.						— Heliotropism and + Geotropism.						Crawling Horizontally in Sea- water.
				Crawling up in Air.		Crawling up in Sea- water.		At Sur- face- Film.		Crawling Down- ward.		Crawling Diago- nally Down- ward.				
				No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
				No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
21½°-19½° C.	90°	15	50	14	28	21	42	9	18	0	0	0	0	6	12	
20½° C.	45°	14	50	7	14	17	34	3	6	7	14	12	24	4	8	
20½° C.	11¼°	10	50	0	0	2	4	0	0	15	30	27	54	6	12	
Total.....		39	150	73 or 48.6%						61 or 40.6%						16 or 10.6%

At the angle of 90°, none were positively geotropic and only six individuals out of 50 crawled horizontally in sea-water (possibly due to the effect of light). At the angles of 45° and 11¼°, the number showing "positive geotropism" increased, as would be expected. At the end of one minute, 21 individuals out of 150 (14 at 90° and 7 at 45°), as shown in the first column of negative geotropism, crawled upward clear through the surface-film of sea-water into the air. 12 individuals (9 at 90° and 3 at 45°), as shown in the last column of the same, crawled upward until they reached the surface-film of sea-water, and then

crawled horizontally. Was this due "to the action of the film of water," as Haseman claims? The question will be answered after consideration of a few other experiments.

Experiment B.—The next series of experiments was of the same nature as the above, but the animals were placed with their heads upward instead of downward at the beginning. The results given in Table VI. show that the starting position, that is, placing the animal head downward or upward, at the beginning of the experiment, makes a difference in the result.

TABLE VI.

GEOTROPISM OF SNAILS IN AND OUT OF SEA-WATER IN DIFFUSE DAYLIGHT AT DIFFERENT ANGLES OF INCLINATION OF A GLASS PLATE.

At beginning of experiments each head placed pointing *upward*. Table shows results after one minute.

Temp. of Sea-water.	Angles.	No. of Trials.	No. of Animals.		— Geotropism and + Heliotropism.								+ Geotropism and — Heliotropism.				Crawling Horizontally in Sea-water.
					Crawling Up in Air (No Hesitation at Surface).	Crawling Up in Sea-water (Not yet at Surface).	Hesitated at Surface then Crawled Through into Air.		Hesitated at Surface and Crawled Horizontally.		Crawling Downward.	Crawling Diag. Down.					
No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%				
19½° C.	90°	14	50	23	46	0	0	6	12	11	22	0	0	0	0	10	20
21¼° C.	45°	13	50	19	38	12	24	3	6	5	10	1	2	8	16	2	4
21½° C.	11¼°	10	50	3	6	24	48	0	0	0	0	8	16	11	22	4	8
Total		37	150	106 or 70.6%								28 or 18.6%				16 or 10.6%	

Here, again, eleven individuals at the angle of 90° and five at 45° crawled horizontally beneath the surface-film of sea-water. Besides these, six individuals at the angle of 90° and three at 45° "hesitated" at the surface-film when they reached it, and then crawled upward through the film. This constitutes a puzzle for the surface-film theory. But let us see further.

Experiment C.—Similar experiments were made in direct sunlight. The glass plate in the aquarium was placed at 45°, which made it parallel to the rays of sunlight as nearly as possible. The outside and bottom of the cylindrical glass aquarium were surrounded by black cloth as already stated; and two sections, *a* and *b* (see Fig. 3), separated within by the glass plate, were

covered above so that the sunlight penetrated parallel to the glass plate and through the open portion, *c*. So arranged, the intensity and direction of the rays of the sunlight had to affect the reaction of the snails to gravity.

Since the animals were negatively heliotropic, it was expected that most of them would crawl downward in this arrangement. Their heads, therefore, were placed upward at beginning, so that definite movements of orientation could be observed. The

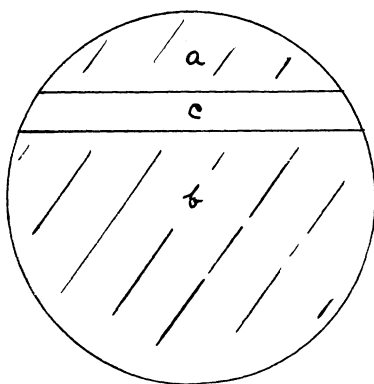


FIG. 3.

results after one minute were as follows: Of 50 animals in 15 trials, 5 or 10 per cent. had crawled upward, all diagonally; 37 or 74 per cent. had crawled downward, 22 of them being well oriented and 15 diagonally; 8 or 16 per cent. crawled horizontally and consequently across the lines of direction both of light and of the effective component of gravity.

The predominance of downward movement was no doubt due to the intensity and direction of the sunlight. This point becomes clearer in the next experiments, but it is clear that the surface-film has nothing to do with such reactions.

Experiment D.—With the same point in mind, other experiments were made in a similar way, but the animals were placed about 1.5 cm. above the surface of the sea-water. In this case 29 individuals out of 50 oriented themselves downward, and crawled in that direction through the surface-film of sea-water into it. Three crawled horizontally at the surface-film instead of going into the sea-water. 18 or 36 per cent. crawled upward.

5. *The Effect of the Surface-film of Sea-water.*

The last of this series was planned in a little different way from the above, entirely excluding light.

As a preliminary test, the snails were placed on the glass plate at the angle of $56\frac{1}{4}^{\circ}$ in the aquarium, which was half filled with sea-water. When those crawling upward reached the surface-film of sea-water and "hesitated," as Haseman calls it, beneath the film, the whole arrangement was covered with the dark box. Ten seconds later, the box was removed for observation. Nearly all that had "hesitated" at the film, were found to have crawled upward *through* the film.¹ Certain individuals at that time had already crawled upward as high as 3 cm. from the film, some 2 cm., and others were just above the film. This experiment was repeated several times and these results were readily demonstrable. Judging from the results, the animals did not seem to have "hesitated" long, after the light was excluded. The "hesitation" of the snails at the surface of sea-water seems to the writer to be due chiefly to the effect of light instead of to action of the surface-film of sea-water. This point also becomes evident after further consideration.

Quantitative experiments were conducted as indicated above. The results are tabulated in Table VII. and show rather complicated conditions.

TABLE VII.

GEOTROPISM OF SNAILS AT THE DIFFERENT ANGLES OF INCLINATION OF A GLASS PLATE IN AND OUT OF SEA-WATER IN TOTAL DARKNESS.

At beginning of experiment each head placed pointing *downward*. Table shows results after one minute and after another half minute.

Temperature of Sea-water.	Angles.	No. of Trials.		No. of Animals.		— Geotropism										+ Geotropism.	Crawled Horizontally in Sea-water.		
						A. After One Minute.						B. After Another Half-minute.							
						Clear Out of Sea-water.		Stopped Just Under Surface-film.		Crawling up in Sea-water.		Clear out of Sea-water.		Underneath Surface-film.				Crawling up in Sea-water.	
No.	%	No.	%	No.	%	No.	No.	No.	No.	No.	No.	After 1 Min.	After 1 Min.						
22° C.	90°	12	50	26	52	18	36	6	12	18	4	4	0	0					
21½° C.	45°	14	50	23	46	11	22	6	12	14	2	1	3	5					
21¼° C.	11¼°	11	50	1	2	13	26	5	10	11	8	5	21	10					
Total		37	150	109 or 72%						67			24	15					

¹ They change their "minds" very rapidly!

"B" covers the activity of those animals which were still below the surface at the end of one minute.

After the first minute, twenty-six individuals at the angle of 90° , twenty-three at 45° , and one at $11\frac{1}{4}^\circ$ were found to have crawled upward through the surface-film of sea-water. Eighteen individuals at the angle of 90° , eleven at 45° and thirteen at $11\frac{1}{4}^\circ$ were just beneath the film of sea-water. And after another half-minute, sixteen individuals at the angle of 90° out of the eighteen, which were beneath the film of sea-water at the end of one minute, nine at 45° out of the eleven, ten at $11\frac{1}{4}^\circ$ out of the thirteen, and one at the same angle which was crawling horizontally at the end of one minute, had crawled upward *through* the film of sea-water. This is significant. At the time of second observation, also, at the angle of 90° two individuals out of six, which were crawling upward *in* sea-water at the end of one minute, at 45° five out of six, and at $11\frac{3}{4}^\circ$ one out of ten which were crawling horizontally at the end of one minute, had crawled upward *through* the film. But at the angle of 90° two individuals out of eighteen which were beneath the film at the end of the first period, at 45° two out of eleven, and at $11\frac{3}{4}^\circ$ three out of thirteen, that is, only seven individuals altogether out of 150, *still remained* beneath the film even at the end of the second period. This is decidedly contrary to the surface-film theory. And at the angle of 90° two individuals out of six, which were crawling upward in sea-water at the end of the first period, at $11\frac{3}{4}^\circ$ four out of five, and at the same angle one which crawled downward in the first period, were beneath the film at the end of the second period.

Referring again to the observation of Haseman that "during a falling tide, some snails are crawling down beneath the surface, some with the surface, and some above the surface" (4, p. 120), and which Haseman claims is "due to the action of the film of water," but not "to either geotropism or phototaxis," the writer is inclined to draw the conclusion based on the results of the series of the experiments above, that the movements of the snails in question are not due, directly, if at all, "to the action of the film of water," but to geotropism and heliotropism. In nature, especially in the daytime when the sun is shining, a considerable part would be played by heliotropism, as Mitsukuri already observed.

Furthermore, in the above experiment, even the seven individuals, that still remained beneath the film at the end of the second period, and whose failure to penetrate the film seems to favor the surface-film action theory, may be considered in a different way. The effect of light having been excluded, their failure to emerge might be due to the susceptibility of these individuals to buoyancy when they had to crawl out of sea-water. This must be taken into consideration as has been shown. It might also in combination with the effect of light explain the behavior of those animals that crawled horizontally beneath the film, or that "hesitated" there, as shown in a number of the preceding tables. Whatever may be the explanation and even if one attributes the slight hesitation to the film itself, it is evident that it has very little effect in determining the total behavior of the animals.

6. *The Effect of Chemicals.*

Besides the above experiments, attempts were made to control the negative geotropism of the snails by chemicals, especially by salts and acids. But all were unsuccessful, except possibly an alcohol experiment. Five snails were placed in a finger bowl containing 100 or 150 c.c. sea-water, to which about 10 c.c. of 95 per cent. alcohol were added without stirring. The finger bowl was shaded. The animals crawled upward on the vertical wall of the bowl, but as soon as they reached the upper layers they turned round, and crawled downward. The negative geotropism was thus apparently reversed. But if the alcohol and sea-water were well mixed by stirring, the reversal was not definite and the experiment was not followed further.

IV. DISCUSSION.

That *Littorina littorea* is negatively heliotropic was first shown by Bohn (1), and this fact has been confirmed by the present writer. Morse, however, has published puzzling conclusions from his observations on this species. He states: "During the days of June, they were, as a rule, *negatively* phototactic, and as *night* approached, they became *positively* phototactic. However after July 18, the preponderance of *positive phototaxis during the day* was very noticeable. This period of transition corre-

sponded to the time of change from spring to neap tide, during which the specimens out *on the rocks* were exhibiting a corresponding change in phototaxis, for the water did not reach them; their behavior tallied with the description of Mitsukuri, who showed that when desiccated, periwinkles became positively phototactic, and when wet, turned negatively phototactic" (14, p. 145).¹

Unfortunately, Morse has given no description of his methods of experimentation. But, judging from his statements, he has entirely overlooked the effect of gravity on the animal, as Mitsukuri did. Was not the supposed "positive phototaxis" "after July 18" really an effect of gravity? *Littorina littorea* does not, in the writer's opinion, crawl upward "on the rocks" on account of positive heliotropism, but on account of negative geotropism and *in spite of* negative heliotropism, which is the unmistakable reaction of the animal to light. Negative heliotropism in the animal is demonstrable even at "night," if the experiment is conducted on a horizontal surface, and if there is any source of light present. The writer believes that Morse's statement that "as night approached, they became positively phototactic" is incorrect. What really happens is this: As the light stimulus diminishes, the gravity stimulus becomes preponderant and the animals are controlled by their negative geotropism.

Frandsen, as already stated, proposes two factors for the determination of geotropism in the slug. The second will be considered first. "*All the conditions being the same,*"¹ he says, "it is this factor (the relative proportions of the length of the anterior and the posterior regions of the animal's body) which 'determines whether the head end will be directed up or down.' If the ratio of the length of anterior to posterior region of body is 2 : 3, or more, and the mucus is of good quality and sufficient quantity, the slug will be positively geotactic. If the ratio is 3 : 5, or less, the animal will usually migrate upward, and the nearer the ratio approaches 1 : 2 the more apt is the slug to respond negatively. . . . All slugs have a natural tendency to move towards the earth. This tendency is masked in the animals which are negatively geotactic on a glass plate by the greater pull of gravity

¹ Italics not in the original.

on the disproportionately larger and heavier posterior region of the animal" (3, p. 205).

Judging from these statements, the center of gravity must lie somewhere in the posterior region of the animal's body. In other words, the posterior region is *heavier* than the anterior. According to Frandsen, the negative geotropism of the animal "on an inclined glass plate," however, is not due to the heaviness of the posterior region, but to "the relative proportions of the length of the anterior and the posterior regions of the animal's body." In short, Frandsen's idea may be expressed thus: The longer (and heavier?) posterior region being pulled by the constant force of gravity, the slug becomes positive to it at the minimal resistance in favor of the ratio above mentioned; on the other hand, it becomes negative at the maximal in disfavor of the ratio. In the latter sense, the "resistance theory," of course, approaches the "mechanical theory."

As pointed out before, this seems to be fairly supported by the results obtained by the writer, which were given in Tables II., III. and IV. This explanation is, however, focused to a limited group of facts; because the snail becomes negative to gravity on the nearly horizontal surface of a glass plate, where the minimal resistance should be expected. This fact is opposed to Frandsen's conclusion. Furthermore, as has already been shown, many snails on the dry wooden plate at the angle of 90° of inclination oriented themselves downward and crawled in that direction, even though in so doing, they met a great mechanical difficulty on account of the heavier posterior region. If the mechanical theory of Frandsen is true, they were under the most favorable conditions for crawling upward instead of downward. This was not, however, the case. Was this because of the first factor of Frandsen, that is, "the quantity and quality of the slime secreted" (3, p. 205). The second factor in question is by no means separable from the first. Both go together. To make Frandsen's statement clearer, therefore, it may be expressed as follows: "The relative proportions of the length of the anterior and the posterior regions of the animal's body" "being the same, it is this factor," that is, "the quantity and quality of the slime secreted," "which determines whether the head end will be directed

up or down." It is fair to examine the table (V.) which is given by Frandsen based on his results. Take the animal No. "13," on which the series of observations, "a" and "b" were made. The condition of the animal was "active" in series "a" and also in series "b," that is, it was under the "same" condition. Being the *same* individual, theoretically there was no difference in the "ratio." Nevertheless, Frandsen obtained *different* results in "a" from "b." Moreover, he shows *different* results in the *same* individual under the *same* condition and in the *same* series of observations, "a" or "b." This is more striking in the animal No. "23," on which the series of observations, "a," "b," "c" and "d," were made under the *same* condition, "good." But he obtained 64.2 per cent. of negative geotropism in series "a," 62.5 per cent. in the "b," 100 per cent. in the "c," and 100 per cent. in the "d." In other words, the *same* individual under the *same* condition was, at least, 35.7 per cent. positive in "a," 37.4 per cent. in "b," and 0 per cent. in "c" and "d." This kind of variation is also found in the animals Nos. "8," "24," "25" and "27." If so, "all the conditions being the same," it is not entirely the first factor, nor the second, "which 'determines whether the head end will be directed up or down,'" but there must be something else besides these two factors, which makes the response variable. Frandsen does not seem, therefore, to be justified even by his experimental data in his conclusions. And strictly speaking, the so-called mechanical theory of geotropism seems to the writer to be misleading in any case, because it is not a living response to stimulus but a purely mechanical one which would be seen as well in the dead organism, if it could be moved. This is no tropism at all.

In this respect, therefore, the writer is inclined to take Davenport and Perkins's conclusion into consideration, as, at least, one of the factors, that is, "some internal condition of the individual." Without this "internal," or physiological, factor, it is difficult to explain why geotropism varies in the different individuals and also in the same individual at the different angles of inclination of the same support and the same angle of inclination of different supports.

Haseman's conclusions demand close consideration on several

points. Haseman states: "Even more interesting is the fact that when, with a vertical surface, a stone, upon which snails were crawling at random, was raised out of the sea, the snails always followed the vanishing film of water even when the vertical surface was rotated through an angle of 180° . In this case, the rotation of the vertical surface would reverse the direction of motion of the film of water and the snails would at once turn around and follow it. But if most of the water was previously removed from the surface of the stone, in order that the film might entirely disappear before the snails (which were crawling downward in the direction of the vanishing film) had reached the lower surface and if, as the film was drying up, the vertical surface was rotated through an angle of 180° , the snails continued to crawl for some time in the direction in which they had started. In other words, the snails crawled upward instead of downward. They continued to crawl thus until the rough surface, food and moisture either deflected or stopped their movements. In the above experiment, the mere turning of the moist but filmless surface through an angle of 180° does not seem adequate to reverse at once the reaction to gravity and light, if either of these have a direct influence on the rhythmical movements of *Littorina*" (4, p. 116).

Certainly this is not a simple matter. In the first phase, Haseman does not state, where "the above experiment" was conducted, what condition of sunlight or diffuse daylight, there was, and if the experiment was in sunlight, in what direction the rays were falling and so on. His description as well as experiment is not at all accurate. Judging from the above description, however, he seems to have conducted the experiment "in nature," and so in sunlight. If so and if the sun were fairly above, it is small wonder that "when the vertical surface was rotated through an angle of 180° ," thus rotating the motion of the film of water, "the snails would at once turn around and follow it," since the snails are negative to light, as has been shown. In the case of Haseman where the film was reversed, in which "the vertical surface was rotated through an angle of 180° ," and "the snails continued to crawl for some time in the direction (upward) in which they had started," another explanation is possible. The

snails being negatively geotropic, the direction and intensity of sunlight were not at the time of this experiment presumably in favor of the reversal of negative geotropism. Therefore, "the snails continued to crawl" "upward instead of downward." This is, of course, reasoned upon the results which were obtained by the writer. At any rate, Haseman seems not to have checked the counteracting forces of gravity and light and consequently all his experiments are unreliable.

One afternoon from four to six o'clock, Dr. Irving A. Field and the writer made special observations of tidal (rising) influence upon the snails at the south shore of Ram Island. The animals were found in large numbers covering a pair of long square beams which formed an inclined railway. These beams presented both vertical and sloping surfaces. In this vicinity there were also rocks and stones of various shapes, their surfaces sloping at many different angles on which numerous snails—oriented with their heads upward—were exposed in *dim* sunlight. When the tide rose higher and higher with no waves and reached to the areas where the animals had been exposed so long that their outer surfaces were completely dried, nearly all of them, if not the entire number, gradually turned head downward and crawled in that direction; some of them moved downward several inches from the original spots, while some others moved about "at random" as if they were seeking food; and still others turned downward when the surface-film of sea-water came in contact with them, while many did so after the surface-film had passed over them to the extent of 0.5 or 1 cm., more or less. If the snails follow "the direction of motion of the film of water," and also, if light has no influence on the rhythmical movements of *Littorina*, as Haseman claims, why did not the snails "crawl upward instead of downward"? Thus considered, it becomes evident that Haseman's observation, or experiment, was not accurate, while Mitsukuri's is, in this respect, confirmed by the writer.

It is very strange to note that Haseman has no notion of the influence of gravity on the snails, although he has observed phenomena which would naturally remind one of it. "When individuals are left high and dry on vertical surfaces during low

tide," he says, "they come to rest 'directed upward,' *i. e.*, with their heads toward the sky. This is true for all sides of the stones and is obviously due to the shape of the apertures of the shells which makes it far easier for exposed individuals to cling thus to vertical surfaces" (4, p. 117). How does he know that "the shape of the aperture of the shells" makes it easier to cling to vertical surfaces? Is it not rather true that the natural tendency of negative geotropism of the snails, favored by the *heavier* posterior region of the shells instead of the shape of the aperture, "makes it far easier for exposed individuals to cling thus to vertical surfaces"? This sounds more reasonable and nearer to the fact than Haseman's supposition.

V. SUMMARY AND CONCLUSIONS.

1. *Littorina littorea* crawls up the vertical (inside) wall of a beaker in a dark aquarium, though the sea-water be better supplied with oxygen at the bottom than at the top. It is negatively geotropic.

2. This snail is negatively heliotropic.

3. The posterior region of the snail has a greater specific gravity than the anterior region.

4. In sea-water, the larger the angle of inclination (to the horizontal) of the surface on which the animals move the larger is the number of negatively geotropic animals; and the smaller the angle of inclination, the larger the number of animals which move downward and are perhaps positively geotropic.

5. In the air, the number of animals showing negative geotropism is always higher than that in the sea-water.

6. On a ground glass plate, the animals are less negatively geotropic than on a plain glass plate.

7. On a dry plain glass plate, a number of individuals oriented positively and crawled downward even at the angle of 90° (vertical) though this never happens on the moist plate. This is more striking on a dry wooden plate.

8. When the animals are placed with their heads down on a dry wooden plate, the highest percentage of positive geotropism is obtained.

9. The snails "hesitate" at the surface-film of sea-water, when light is not excluded.

10. In the direct sunlight, the snails are apparently more positively geotropic than in darkness, due to the fact that they are negatively heliotropic.

11. In the direct sunlight, 58 per cent. of the animals orient themselves head downward and crawl in that direction through the surface-film of sea-water into it.

12. In darkness, the snails, which "hesitated" at the surface-film of sea-water in the daylight, crawl upward *through* the film.

13. From the experimental results which the writer has obtained, he concludes that neither the mechanical theory, nor the pressure theory, nor the resistance theory is adequate to explain the phenomenon of the negative geotropism of *Littorina littorea* but a physiological one, that is, the statocyst or statolith theory. This theory is the more likely since these snails have statoliths (17, pp. 119-120). The writer, however, has no direct evidence, at present, in favor of the statolith theory. He is led to accept it largely by the method of exclusion. Furthermore evidence from many sides based on the experiments of the writer causes him to conclude that the surface-film theory is also not correct.

In conclusion, the writer wishes here to acknowledge his indebtedness to Professors Walter E. Garrey, Ralph S. Lillie, and Elias P. Lyon, for their valuable suggestions and criticism on his experiments at the Marine Biological Laboratory at Woods Hole, Mass., during the summers of 1912 and 1913. His thanks are also due to Professor Frank R. Lillie for the privileges of the Laboratory and to Professor Lyon for criticism and suggestions in the preparation of manuscript.

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